

Species	Sex	2N	N (I)	N (II)	Author
<i>Aranea sexpunctata</i>	♂	—	11+X <sub>1</sub> X <sub>2</sub>	— —	HACKMAN '48
♂ <i>japonicus</i>	♂	—	11+X <sub>1</sub> X <sub>2</sub>	11 13	SUZUKI '51a
♂ <i>mitificus</i>	♂	—	11+X <sub>1</sub> X <sub>2</sub>	11 13	♂ ♂
♂ <i>opima</i>	♂	24	11+X <sub>1</sub> X <sub>2</sub>	11 13	♂ ♂
♂ <i>scylla</i>	♂	14	6+X <sub>1</sub> X <sub>2</sub>	6 8	♂ ♂
♂ sp.	♂	24	11+X <sub>1</sub> X <sub>2</sub>	11 13	♂ ♂
♂ <i>ventricosus</i>	♂	46	22+X <sub>1</sub> X <sub>2</sub>	— —	♂ ♂
♂ <i>fuscocoloratus</i>	♂	—	11+X <sub>1</sub> X <sub>2</sub>	11 13	♂
♂ <i>saganus</i>	♀	26	—	—	♂
<i>Larinia punctifera</i>	♂	24	11+X <sub>1</sub> X <sub>2</sub>	— —	♂
<i>Zilla stroemi</i>	♂	—	11+X <sub>1</sub> X <sub>2</sub>	— —	HACKMAN '48
Fam. Mimetidae					
Subfam. Mimetinae					
<i>Ero japonica</i>	♂	24	11+X <sub>1</sub> X <sub>2</sub>	— —	SUZUKI

## DISCUSSION

## 1. Number of spiders species studied cytologically

The cytological studies of spiders have been carried out by many workers, among which the earlier investigations were reported by CARNOY (1885), WAGNER (1896 a,b), WALLACE ('00, '05, '09), BÖSENBERG ('04), MONTGOMERY ('05, '07) and BERRY ('06). Following these authors PAINTER ('14), SOKOLSKA ('25), WARREN ('25, '26, '28, '29, '30) and HARD ('39) contributed to this field. Recently remarkable reports have been published by many workers such as REVELL ('47), PÄTAU ('48), HACKMAN ('48), SUZUKI ('49, '50a,b, '51a,b, '52a,b,c, '53, '54 and present paper), SUZUKI and OKADA ('50), SHARMA ('50) and BOLE-GOWDA ('50, '52). In particular HACKMAN and the present author studied the chromosomes of vast number of spiders. The total number of species studied cytologically by these workers amounts to 181 species of 90 genera belonging to 26 different families of all three suborders. The number of species and families studied are shown in the following table.

Table III. Number of species and families studied cytologically.

Family	No. of genera	No. of spp.	Family	No. of genera	No. of spp.
Liphistiomorphae			13. Thomisidae	9	21
1. Liphistiidae	1	1	14. Salticidae	15	21
Mygalomorphae			15. Oxyopidae	3	6
2. Aviculariidae	1	1	16. Lycosidae	7	24
3. Atypidae	1	1	17. Pisauridae	2	8
Arachnomorphae			18. Agelenidae	4	10
4. Uloboridae	2	2	19. Argyronetidae	1	1
5. Dictynidae	1	2	20. Urocteidae	1	1
6. Amaurobiidae	1	1	21. Theridiidae	7	8
7. Dysderidae	1	1	22. Linyphiidae	3	8
8. Pholcidae	2	2	23. Micryphantidae	1	1
9. Drassidae	7	9	24. Tetragnathidae	2	5
10. Clubionidae	4	12	25. Argiopidae	7	25
11. Anyphaenidae	1	2	26. Mimetidae	1	1
12. Sparassidae	5	7	Total	90	181

(Thomisidae includes Misumeninae and Pilodrominae.)

Most of these species were studied by HACKMAN ('48) and the present author; namely, 69 species (17 families) were researched by HACKMAN, and 90 species (21 families) by me. The number of species of spiders whose chromosomes have been counted with certainty or in considerable degree of accuracy is 177, and the spiders in which sex-chromosomes have been studied are 179 species. As is well known in the Table III the great majority of the species studied belong to the modern spiders constituting the suborder Arachnomorphae, for example, 178 species, i. e. 98.3 per cent are modern spiders. In Liphistiomorphae and Mygalomorphae only three species, i. e. 1.7 per cent are recorded. It is a natural consequence if we know systematic feature of these three suborders. The investigation of such different suborders, however, would be of much importance to know the chromosomal evolution in spiders.

In the Arachnomorphae Argiopidae, Lycosidae, Salticidae and Thomisidae are well known cytologically, which followed by Clubionidae, Agelenidae, Drassidae, Pisauridae, Theridiidae and Linyphiidae.

In the following section I will give general discussion concerning the main problems of chromosomes in spiders. For the convenience of understanding, the general review of chromosomes in different families of spiders will be described at first.

## II. General review of chromosomes in different families of spiders

**Liphistiidae:**— This is the only one living family in the Liphistiomorphae, which comprises most primitive spiders known as living fossils. The chromosomes of this family are extremely intriguing. Only a single species *Heptathela kimurai* has been known cytologically in this report. The species shows the diploid number 94, the chromosomes are very small in size. The number is the largest among 177 species so far investigated. Between the present species and all the remaining ones exist great deviations of chromosome number. The species is considered to have an XXO-system of sex-determination.

**Aviculariidae:**— This is one family of the second suborder Mygalomorphae, which is also regarded as to be considerably old. One species *Dugesiella* was studied by PAINTER ('14). It bears  $n=23$  and an XXO-system. HACKMAN ('48) criticized that the species has XO-system and the haploid number 22. At any rate its number is considerably large among spiders.

**Atypidae:**— This family also belongs to the Mygalomorphae. The morphology and habit seem to be very old. One species *Atypus karschi* was studied in this paper. The species bears  $2n=44$ ,  $n=23$ , and XXO-system. This number is equal to that of the previous species of *Dugesiella*. The mitotic chromosomes are very small, which show similar appearance to *Heptathela kimurai*.

All the following families belong to the same suborder Arachnomorphae.

**Uloboridae:**— The two species of *Uloborus* and *Miagrammopes* were researched in the present article. Both species show  $2n=22$ ,  $n=12$ , and with XXO-type. In *Miagrammopes* females the occurrence of 4 X's was demonstrated by direct observation. As cribellate spiders have never been fully studied cytologically, the comparison with allied species is rather hasty, but some cytological results obtained indicate that no remarkable similarity exists between the Uloboridae and other cribellate families. Namely the number and shape of chromosomes of Uloboridae differ entirely from those of Dictynidae and Amaurobiidae. It is interesting that in cytological characters the Uloboridae shows rather close resemblance to the Argiopidae. It is worth noting that systematically the present family is placed near the Argiopidae by PETRUNKEVITCH ('28), SAVORY ('28) and some others.

**Dictynidae:**— Two of the *Dictyna* are studied by HACKMAN ('48) and by me in this paper. Both species males possess  $2n=24$ ,  $n=13$ , and with XXO-system. Of the diploid chromosomes 22 are autosomal, which are of metacentric type, the remaining two are sex-chromosomes, of acrocentric type. The occurrence of metacentric elements is so rare in spiders that the karyotype of the *Dictyna* should be noticed. If both

arms of the metacentric elements are counted as two, the diploid number of the *Dictyna* becomes 46, which is the largest number except the *Heptathela kimurai*.

**Amaurobiidae:**— One of *Amaurobius* is known cytologically by PAINTER ('14). It shows the haploid number of 18 and an XXO-mechanism. Because of the failure of obtaining mitotic chromosomes it is not yet certain whether they are of acrocentric type or not, but judging from the PAINTER's picture they are likely to be of acrocentric type. This family also belongs to the Cribellatae and the chromosome number of one species is relatively high.

**Dysderidae:**— The present and all the following families belong to the Ecribellatae. The Dysderidae is ranked on the first position in the ecribellate spiders. Even the arachnologists who do not recognize the separation of cribellate and ecribellate forms place the family on the lower situation in the Arachnomorphae. Only a single species *Ariadna lateralis* is investigated in the present work, the haploid number of which is only 4 and an XO-system is found. The autosomes are regarded as to be metacentric. This number is the smallest among the species so far studied. The chromosomes in the maturation divisions are huge, it is probable that one element of this species corresponds to two or more chromosomes of the allied forms. Although it is not published, by HACKMAN *Segestria senoculata* shows  $2n=14$ , ten of which are metacentric and the rest four (including 2 X's) acrocentric. The karyotype of this kind is equal to *Aranea dumetorum* and *A. scylla* reported by HACKMAN ('48) and SUZUKI ('51) respectively. The chromosome features of the two species of this family are thus extremely characteristic. So far as chromosomes are concerned, the species are regarded as to have been highly developed, contrary to the taxonomic result.

**Pholcidae:**— One species of *Spermaphora* and two species of *Pholcus* were researched cytologically by PAINTER ('14) and SUZUKI in this paper. An XXO-system is characteristic for both genera, the chromosome number is counted only in *Pholcus crypticolens* by me, which is  $2n=24$  and  $n=13$ . In general the chromosomes are very small, which renders the observation very difficult. In cytological features *Pholcus crypticolens* very much resembles to the members of *Dictyna* of cribellate forms. Here also, all the autosomes (11 pairs) are regarded as metacentrics. It is of much interest that the *Pholcus* and *Dictyna* show similar but aberrant karyotypes, contrary to their different systematic situation. Now the system of classification reported by PETRUNKEVITCH ('28) and SAVORY ('28) is worth noticing. They do not recognize the separation of cribellate forms, by them the Pholcidae and Dictynidae are placed close to each other in the Trionycha, especially SAVORY established a Tribe Retitelariae which comprises Dictynidae, Theridiidae, Pholcidae,

### Linyphiidae and Archaeidae.

**Drassidae:**— The chromosomes of nine species belonging to 7 genera were published (PAINTER, '14; HACKMAN, '48; SUZUKI, in this paper). All species possess similar chromosomal condition, namely with the haploid number 12 and sex-determining mechanism of an XXO-type. The chromosomes are acrocentrics. The mitotic chromosomes of one species of *Drassodes* studied by me are very small rods. On the other hand one species of *Haplodrassus* studied by HACKMAN show very large meiotic chromosomes.

**Clubionidae:**— The chromosome condition of this family were fully described in my previous report (SUZUKI, '52a). Twelve species belonging to 4 genera were investigated cytologically. The chromosomes are always of acrocentric type and exists an XXO-mechanism without exception. The haploid numbers are 12 in 7 species, 13 in 1 species and 14 in 3 species.  $N=14$  is characteristic for the *Chiracanthium* and 12 for the *Clubiona*.

**Anyphaenidae:**— Two species of *Anyphaena* were reported by PAINTER ('14) and HACKMAN ('48). The haploid number is 11 in one species and 14 in the other. Both species bear an XXO-system. By HACKMAN the chromosome size of *Anyphaena* is small and nearly equal to that of *Clubiona*.

**Sparassidae:**— The chromosome study of this family were stated in detail in my second report (SUZUKI, '52a), afterwards one important paper was published by BOLE-GOWDA ('52). Thus the cytologically known species are 7 belonging to 5 genera. In general the chromosomes are remarkably large in size. The haploid numbers vary from 11 to 23, of which 11 occurs in one species, 19 in one species, 22 in four species and 23 in one species. In 6 out of 7 species the chromosomes are entirely acrocentric, the remaining one, *Heteropoda sexpunctata* is exceptional, which bears 19 metacentrics and 2 acrocentrics in diploid set (BOLE-GOWDA, '52). Three kinds of sex-determining mechanisms, XO, XXO and XXXO-type are present, of which XXXO-type is found in 5 species, XXO-type, in *Olios lamarcki* and XO-type, in *Heteropoda sexpunctata*. By BOLE-GOWDA a single X-element of *H. sexpunctata* is metacentric. The chromosomes of this family thus exhibit remarkable characteristics, further investigations are very intriguing. The presence of 6 X's in the female is fairly demonstrated by direct observation in *Heteropoda venatoria* (SUZUKI and OKADA, '50). So far as the chromosomes are concerned some close resemblance can be found between the Sparassidae and the Agelenidae.

**Thomisidae:**— General aspect of chromosomes in this family was stated in my previous paper (SUZUKI, '52a). Twenty-one species belonging to 9 genera are recorded cytologically by many authors. This family is

divided into two subfamilies, Misumeninae (=Xysticinae) and Philodrominae. Both subfamilies show characteristics of considerable degree in chromosomes. For example, haploid number of 12 and XO-system are characteristic for most of Misumeninae, on the other hand  $n=15$  and XXO-system for the Philodrominae. In cytological aspect *Oxytate*, *Diaea*, *Tibellus* are regarded as intermediates between the both subfamilies. In most species belonging to Philodrominae the two X's show difference in size; the difference may be great in some species or less great in others.

**Salticidae:**— The chromosomes of 14 species have been researched in the present paper, so that the cytologically studied species amount to 21 species of 15 genera. Except a single species *Myrmarachne formicaria* reported by HACKMAN ('48) all the species show similar chromosome condition, i. e.  $2n=28$ ,  $n=15$  and XXO-system are characteristic for most of the species. HACKMAN's *Myrmarachne formicaria* bears exceptionally  $n=12$ , and XO-system. All chromosomes are acrocentrics. It is interesting that the chromosomes of Japanese *Myrmarachne japonica* differ from those of Finnish *Myrmarachne formicaria*. But it is more or less doubtful if HACKMAN's description of Finnish *Myrmarachne* is correct, because in his material no mitotic nor second metaphase chromosomes have been obtained, on the other hand in Japanese *Myrmarachne* the chromosome number and sex-chromosomes have been observed in detail throughout all stages of spermatogenesis as well as oogenesis. The chromosomes of this family, in particular those of *Plexippus*, are extremely large and favourable for observation. Furthermore, the chromosomes of *Plexippus* exhibit some characteristic forms. At any rate the numbers of chromosomes of this family are constant in species studied, except a single species, thus  $n=15$  is regarded as modal number of the family. In this family the chromosomes have been investigated not only in the males, but in females of some species. It is worth noting that polyploid spermatocytes are found in *Hasarius adansoni* and *Icius magister*. In the former tetraploid primary spermatocytes, and in the latter tetraploid primary and secondary spermatocytes are obtained. In both cases such polyploid cells are found, forming solitary cyst in in other respects quite normal testes.

**Oxyopidae:**— The chromosomes of this family were summarized in my second paper (SUZUKI, '52a). Six species of three genera were researched. Five species possess  $2n=21$ ,  $n=11$  and XO-type. The remaining one bears  $2n=28$ ,  $n=15$  and XXO-type. Thus the single X is characteristic for most of the present family. No metacentric elements are present.

**Lycosidae:**— The cytologically studied spiders are 24 species belonging to 7 genera. An XXO-type of sex-determining mechanism is characteristic of all species studied. The chromosome number varies

from 12 to 15, of which 15 occurs in the highest frequency, i. e. it occurs in 13 species, following 14 in 7 species and 12 in 3 species; 13 is recorded only in one species. The number of 15 is particularly characteristic for most of the genus *Lycosa*. It must be noted that microchromosomes are found in some *Lycosa* species, which would play some role in the course of chromosomal evolution. In most cases each of the two X's is equal in length, but not in *Lycosa fluviatilis*, *L. T-insignita*, *L. cinereofusca* and *Trochosa rulicola*, where distinct size difference is found between the X's. It is specially remarkable in *L. cinereofusca*.

**Pisauridae:**— Two species of *Pisaura* and six species of *Dolomedes* were researched cytologically. In general the chromosomes are large and very favourable for study. All elements are of acrocentric type. The haploid number of 15 is characteristic for seven species, the remaining one *Dolomedes fimbriatus* is exceptional, which possesses  $n=13$ . *Dolomedes fontanus* studied by PAINTER ('14) bears one pair of microchromosomes. The sex-chromosomes of XXO-type is commonly present in all members. The sex-chromosomes of this family seem to be smaller pair in the complements, while in other families they are larger ones. During the first division the X's tend to lie on the plate with considerable distance to each other. The chromosome number of females are also determined in *Pisaura lama*, *Dolomedes angustivirgatus* and *D. sulfureus* by me. As far as chromosomes are concerned considerable similarities exist between the Pisauridae and the previous family Lycosidae in accordance with their taxonomic relationship.

**Agelenidae:**— Three species of *Agelena*, five species of *Tegenaria*, one species of *Cryphoea* and one species of *Hahnia*, i. e. totally ten species have been researched cytologically, of which two of *Agelena*, one of *Tegenaria* and one of *Cryphoea* have been described in this paper. All species show rather high chromosome numbers which ranging from 18 to 22 in haploid. Among them 23 occurred in five species, 22 in two and 18 in one. Concerning the chromosome numbers in some species, however, some confusion is seen in different authors. The chromosome number of *Agelena naevia* was first reported as  $2n=40$  by WALLACE ('05), which was corrected as  $2n=ca. 52$ ,  $n=ca. 27$  in her second paper (WALLACE, '09). PAINTER ('14) who studied the same species stated that the chromosome number of *Agelena naevia* was overestimated by her, and regarded the number as about 15 in haploid. On the other hand, HACKMAN ('48) criticized WALLACE's results and recorded its haploid number as about 18. The figures shown by WALLACE ('09) are not so much sharply drawn, that it is rather difficult to criticize strictly the number of chromosomes. A comparison with Japanese *Agelena* species suggests that the number estimated by WALLACE is too high, but those reported by PAINTER and HACKMAN are too low, probably the species

possesses nearly similar number to the Japanese *Agelena*. In *Tegenaria domestica* and *derhami* also exist some inconsistency in chromosome numbers. In this case some taxonomical confusion is involved. HACKMAN ('48) stated that *Tegenaria domestica* is a collective name and *T. domestica* studied by SOKOLSKA ('25) is synonymous to *T. derhami*. In spite of HACKMAN's statement REVELL ('47) recognized the separation of *domestica* and *derhami*, and reported the chromosomes of these two species. It is of no use to describe further on this problem. At any rate there is a difference between the REVELL's and HACKMAN's results on *T. derhami*. The autosome number in haploid set of the spider is 20 by REVELL, but 16 by HACKMAN. The difference is so large that it is not convinced that such difference is caused by local variation. As HACKMAN stated the 16 autosomes seem to be a probable number, so that 20 might be real autosome number of *T. derhami*. Generally speaking the species of this family studied bear high chromosome number. The present family is characteristic not only in chromosome number but also in sex-determining mechanism. Most species, i.e. six out of nine species studied, possess XXO-mechanism and the remaining species, *Tegenaria domestica*, *T. derhami* and *Cryphoea silvicola*, XXXO-mechanism. As regards the three X's of *Cryphoea* full description is given in the foregoing pages. The chromosome number and sex-chromosomes of this family are thus extremely specific; in these characters the present family shows similarity to Sparassidae.

Argyronetidae:— Only a single species was studied by HACKMAN ('48). The chromosomes are too small for the detail to be observed. The haploid number is 13 and XXO-system is present. Systematically the family is included in Lycosoidea together with Agelenidae, Lycosidae and Pisauridae, etc., but apparently no remarkable cytological relationship can be found between the present and the allied families.

Urocteidae:— The chromosomes of a single species *Uroctea compactilis* are mentioned in the present paper. The chromosome number is  $2n=42$ ,  $n=22$  and sex-mechanism is XXO-type. All the chromosomes are of acrocentric type and of considerable size. The general feature of chromosomes resembles those of Agelenidae and Sparassidae. In systematic viewpoint the present family is considered to be somewhat isolated from others, for example, the present family constitutes separate Section in Clubionoidea by BRISTOWE ('38). But in SAVORY's classification the present family together with Amaurobiidae, Agelenidae and some others belongs to the same Tribe Stichotrichiae. In connection with SAVORY's opinion it is very interesting that the chromosome number of the present family is nearly similar to those of Amaurobiidae and Agelenidae.

Argiopoidea:— The following six families are considered to be closely



related to each other, which constitute one Group Argiopoidea or Superfamily Epeiroidea.

**Theridiidae:**— The chromosomes of eight species belonging to seven genera have been studied. In the present paper six species of them have been newly described. The haploid number of 12 is characteristic for six species, which is regarded as modal number of this family. The remaining two species of *Lithyphantes* and *Nesticus* show  $n=13$  instead of 12. An XXO-system is present in all species studied. The chromosomes are always of acrocentric type and in most species very small in size, which makes minute observation difficult. But the species of *Steatoda*, *Ariamnes* and *Lithyphantes* are exceptions, in which the elements are of considerable size. In general the chromosomes of the present family resemble those of Linyphiidae, Tetragnathidae and Argiopidae.

**Linyphiidae:**— Eight species have been surveyed cytologically, one half of which have been reported by me. The chromosomes are acrocentrics and are small in size and in most cases it is rather difficult to obtain good fixation. Most species, i. e. 7 species, possess  $n=13$ , while a single species *Linyphia montana*  $n=24$ . An XXO-type is characteristic for all members studied. The general feature of chromosomes closely resembles those of Argiopidae and Tetragnathidae. The chromosome number of *Linyphia montana* is of much interest, apparently it seems to be tetraploidy. In my opinion, however, it is not so, the chromosomal condition of the species would be analogous to that of *Araneus ventricosus* of Argiopidae. In most of the species studied the epithelial cells of testes show extremely large nuclei, which are regarded as to be high polyploidy.

**Micryphantidae:**— One species of *Gongylidium* has been studied by HACKMAN ('48). The chromosomes are very small and not favourable for observation. The species bears  $n=12$  and an XXO-type. The epithelial cells of testes are of very large polyploid nuclei as in Linyphiidae.

**Tetragnathidae:**— Four species of *Tetragnatha* and one species of *Leucauge* have been investigated cytologically, three of which have been newly stated in the present paper. The two Finnish *Tetragnatha* species show  $n=12$  by HACKMAN, but the two Japanese species of *Tetragnatha* and one *Leucauge* species,  $n=13$ . In my study the chromosome number has been counted exactly in both mitotic and meiotic divisions throughout all the materials, so that the numbers of the Japanese species seem to be more plausible. The chromosomes are so small that one or two elements are apt to be out of sight. The reinvestigation of the Finnish species is desirable. All species bear an XXO-system. The number and shape of chromosomes of this family closely resemble those of the Linyphiidae and some Argiopidae in accordance with their systematic relationship.

**Argiopidae:**— The general feature of chromosomes of this family has already been stated in my first paper (SUZUKI, '51a), but five more species have been newly studied in this paper, so the species investigated amount to 25 species of 7 genera. Except three species all the members show equal chromosome number  $2n=24$ ,  $n=13$ , and XXO-system. Thus  $n=13$  is typical to most of the family. The exceptions are *Aranea dumetorum* (HACKMAN, '48), *A. scylla* (SUZUKI, '51a) and *A. ventricosus* (SUZUKI, '51a). The first two species exhibit  $2n=14$ , 10 of which are metacentrics, the rest 4 (including 2 X's) acrocentrics. The 10 metacentrics are regarded as to correspond to 10 pairs of acrocentrics in the allied species. The third species *A. ventricosus* shows  $2n=46$ ,  $n=24$ . The 44 autosomes of this species are twice the number of that of the allied forms. The details of such aberrant forms were mentioned in my previous report (SUZUKI, '51a).

**Mimetidae:**— One species of *Ero* has been reported in the present article. The chromosomes are of acrocentric type, which are of some characteristic form. The chromosome number is 24 in  $2n$ , 13 in  $n$ , and XXO-mechanism is present.

### III. Variation of chromosome numbers

In the previous section general aspect of chromosomes in different families has been given, here the variation of chromosome numbers in spiders will be mentioned. As stated before the numbers of species whose chromosome numbers have been determined definitely or in considerable degree of accuracy are 177 species belonging to 26 families covering 3 suborders.

The lowest number (unless otherwise mentioned the number means the haploid chromosome number in this section) is 4 in *Ariadna lateralis* and the highest is  $\pm 48$  in *Heptathela kimurai*. Others are ranging between both extremes. HACKMAN ('48) states that the chromosome numbers of spiders vary within comparatively limited range, namely from 8 to 20. My studies, however, reveal that the numbers of chromosomes show remarkably wide range contrary to HACKMAN's report. It is a matter of course that the results differ between the both workers, because HACKMAN's study is devoid of such particular materials as Liphistiidae and Dysderidae.

In animal kingdom the chromosome numbers have been studied in numerous species. In some cases they show very wide range, but within the same group the variation is not so large. As far as published data are concerned, we have only some orders whose chromosome numbers are subject to considerable variation. Such representatives are Lepidoptera, decapod Crustacea and Scorpionida. It is very interesting that the

present order and Scorpionida, both of which belong to the same class, show similar remarkable variation of chromosome numbers.

Although both extremes show remarkable difference, most species of spiders possess rather limited numbers of chromosomes, namely, except *Ariadna* and *Heptathela*, the haploid numbers of the remaining 175 species are ranging between 8 and 24. No species has been found to show the numbers between 24 and 48, thus great bridgeless gap exists between the two numbers.

The frequency of chromosome number is shown in the Table IV and Diagram I.

Table IV. Frequency of haploid chromosome numbers in spiders.

Chrom. no.	Fam.	Spp. no.	Total	%	Chrom. no.	Fam.	Spp. no.	Total	%		
4	Dysderidae	1	1	0.56	14	Clubionidae	3	13	7.34		
8	Argiopidae	2	2	1.12		Anyphaenidae	1				
11	Anyphaenidae	1	7	3.95		Thomisidae	2				
	Sparassidae	1				Lycosidae	7				
	Oxyopidae	5			15	Thomisidae	8	49	27.74		
12	Uloboridae	2	Salticidae	20							
	Drassidae	9	Oxyopidae	1							
	Clubionidae	7	Lycosidae	13							
	Thomisidae	9	Pisauridae	7							
	Salticidae	1	18	Amaurobiidae	1	2	1.12				
	Lycosidae	3	Agelenidae	1							
	Theridiidae	6	19	Sparassidae	1	1	0.56				
	Micryphantidae	1	22	Sparassidae	4	7	3.95				
Tetragnathidae	2	Agelenidae		2							
13	Dictynidae	2		44	24.86			Urocteidae	1		
	Pholcidae	1	23			Aviculariidae	1	8	4.52		
	Clubionidae	1				Atypidae	1				
	Thomisidae	2				Sparassidae	1				
	Lycosidae	1				Agelenidae	5				
	Pisauridae	1	24			Linyphiidae	1	2	1.12		
	Argyronetidae	1				Argiopidae	1				
	Theridiidae	2	48			Liphistiidae	1	1	0.56		
	Linyphiidae	7									
	Tetragnathidae	3									
	Argiopidae	22									
	Mimetidae	1									
	Total						177 spp.				

As shown in the Table IV and Diagram I the highest frequency is 15 (27.74%), 13 (24.86%) and 12 (22.6%), which are followed by 14 (7.34%). Next is 23 (4.52%), 22 (3.95%) and 11 (3.95%). The remaining numbers 4, 8, 18, 19, 24 and 48 are found only in one or two species (0.56–1.12%).

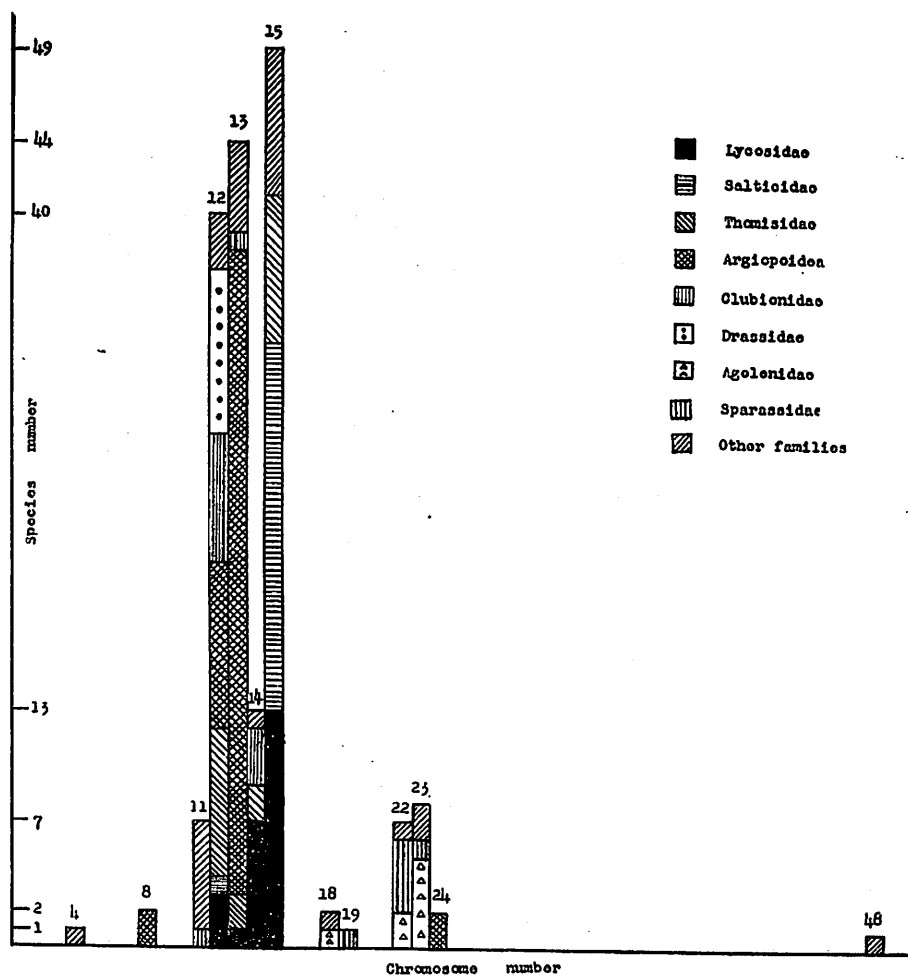


Diagram I. Haploid chromosome number in different groups of spiders. Argiopoidae includes Families Theridiidae, Linyphiidae, Micryphantidae, Tetragnathidae, Argiopidae and Mimetidae.

Generally speaking most of the species studied, i. e. 153 species (87.61%), possess rather low numbers of 11 to 15. The spiders showing the numbers of 18 to 24 are 20 species (11.27%), such numbers are considered to be very significant in the chromosomal evolution; regarding this point further statement will be given in the following pages.

## IV. Morphology of chromosomes

## 1. Shape of chromosomes

In great majority of spiders the chromosomes are of acrocentric type, which are regarded as to bear terminal or subterminal spindle fibre attachment. Such chromosomes are essentially rod shaped. On the other hand metacentric elements are found only in some exceptional cases. By published data and my studies the spiders which possess metacentric elements are the following 7 species of 5 different families.

Argiopidae: *Aranea patagiata* (= *dumetorum*) by HACKMAN ('48); *Ar. scylla* by SUZUKI ('51a).

Dictynidae: *Dictyna arundinacea* by HACKMAN ('48); *D. foliicola* by SUZUKI.

Pholcidae: *Pholcus crypticolens* by SUZUKI.

Sparassidae: *Heteropoda sexpunctata* by BOLE-GOWDA ('52).

Of these both *Aranea patagiata* and *scylla* were already reported in detail (HACKMAN, '48; SUZUKI, '51a). The two species bear  $2n=14$ , 10 of which are metacentrics and the rest 4 acrocentrics. The allied forms of the same genus studied show  $2n=24$ , all of which are acrocentrics. The 10 metacentrics in the two *Aranea*-species are regarded as to be homologous to 10 pairs of acrocentrics in the allied forms. Therefore HACKMAN and SUZUKI concluded respectively that in such cases 10 metacentrics might have been derived from the centric fusion of 10 pairs of the allied forms.

*Dictyna arundinacea* and *foliicola* show quite similar karyotype,  $22V+2R$  in the male. In these cases all the autosomes are metacentrics, while the X's are acrocentrics. However, it is not certain whether the metacentric elements have been produced by centric fusion of two homologous acrocentrics in the allied forms or not, because of lack investigation of the near relatives. As is well known the *Dictyna* is a member of the cribellate forms. In this group some Uloboridae and Amaurobiidae are studied cytologically. The two species of *Uloborus* and *Miagrammopes* belonging to Uloboridae mentioned in the present study show  $2n=22$  and all of which are of acrocentric type. Therefore no similarity can be found between the chromosomes of the *Dictyna* and these two species. *Amaurobius bennetii* (= *sylvestris*) of Amaurobiidae reported by PAINTER ('14) bears the haploid number 18. The number was counted in the second division metaphase. In his figures (PAINTER's Taf. 32 Figs. 82-83) the chromosome elements are packed so closely on the plate that it is rather difficult to count them clearly. And the study was carried out 40 years ago using an old technique. So that it is somewhat doubtful whether his number is quite true or not. In my opinion its

number may be more than 18. If so, the chromosome number of *Amaurobius* becomes approximately similar to the number of chromosome limbs of *Dictyna*. Further investigations in these forms are very intriguing.

The chromosomes of *Ariadna lateralis* are of much interest in many points. The haploid number is only 4 and each element bears remarkably large shape. To my regret no gonial metaphase was obtained, but judging from the meiotic chromosomes the karyotype of the species might be  $6V+1R$ . Seemingly the bivalents are huge and look like rather chromosome blocks. When the chromosomes (bivalents) of *Ariadna* are compared with those of many species with more chromosome numbers, one large element in *Ariadna* seems to be represented by two or more chromosomes in usual species. In Lepidoptera some of great deviations of chromosome number are often found between related species (SUOMALAINEN, '53). Usually in such cases certain single species deviates greatly in chromosome number from the other related species. By SUOMALAINEN in some cases the chromosomes are much larger in the species with fewer chromosomes. And the great deviation in chromosome number is considered to be due to a fragmentation or fusion of the chromosomes (FEDERLEY, '38, '43, '45, SUOMALAINEN, '53). It may be said that such similarity is possible to occur in the present case. Further investigation in the related species is greatly desirable.

It is beyond doubt that metacentric elements are found in *Pholcus crypticolens*. Here all the 10 pairs of autosomes seem to be metacentric as in *Dictyna*. Two allied species *Spermaphora meridionalis* and *Pholcus phalangoides* were studied by PAINTER ('14), but no favourable figures were obtained by him. Therefore the relationship between the *Pholcus crypticolens* and the near relatives is obscure.

The karyotype of *Heteropoda sexpunctata* was reported by BOLE-GOWDA ('52), which is  $19V+2R$  in the male. In this case a single X is also metacentric. The allied species *Heteropoda venatoria* (SUZUKI and OKADA, '50; BOLE-GOWDA, '52) and *H. forcipata* (SUZUKI, '52a) males possess 41 acrocentric elements in diploid set. So that BOLE-GOWDA states that 38 acrocentric autosomes of *venatoria* correspond to 18 metacentrics plus 2 acrocentrics (autosomes) in the *sexpunctata*. The remaining metacentric X-element also is regarded as to have originated by the centric fusion of 2 out of the 3 acrocentric X's in *venatoria*.

The above descriptions are concerned largely on the metacentric elements, in the case of acrocentric elements only a few aberrant forms are found. Those are *Plexippus*-species belonging to Salticidae. As stated in the foregoing pages they show remarkably large chromosomes, which are elongated rods and with some appendages at their proximal end. In *Plexippus setipes* most chromosomes bear setae, which are long

in some elements and short in others, and sometimes are furnished with minute globules at apices. The occurrence of these aberrant chromosomes in animals is very interesting. Further careful observations are desirable in future.

## 2. Size of chromosomes and cell plates

Remarkable variation can be found in the size of chromosomes and cell plates of different species. It is somewhat difficult to determine the accurate size of chromosomes, because their size and shape are not always constant, but vary more or less in different figures of the same species. Generally speaking, however, some are of smaller, some others of medium and still some others of larger size. The smaller chromosomes are encountered in the members of Liphistiidae, Atypidae, Dictynidae, Pholcidae, Theridiidae, Linyphiidae, and Tetragnathidae, etc. In these families most of the species show very smaller chromosomes. But even in such groups Theridiidae and Linyphiidae contain some species with medium or large sized chromosomes. For example, in Theridiidae, *Lithyphantes* bears medium sized elements and *Ariamnes*, very large ones, though *Crustulina*, *Enoplognatha* and *Theridium* exhibit, very small sized ones.

The chromosomes of Dysderidae, Sparassidae, Salticidae, Lycosidae, Agelenidae and Urocteidae are very large, especially all the species of Sparassidae, Agelenidae and Urocteidae possess very large size without exception. The greatest size is found in *Thelcticopis* of Sparassidae (SUZUKI, '52a) and in *Plexippus* of Salticidae. The spiders of the remaining families have medium sized chromosomes.

The sizes of cell plates also are subject to considerable variation. They are characteristic in some degree in families. Generally speaking the species with larger sized chromosomes exhibit larger cells, with some exceptions, in which the cell plates are notably large, although the chromosomes are very small in size. The most favourable examples of such species are *Heptathela kimurai* and *Atypus karschi*, especially the cell plates of the former are enormously large, the largest in spiders ever studied. It seems more probable that some correlation exists between the whole volumes of chromosomes and the cell plate.

## V. Evolution of chromosome numbers

As stated above the numbers of spiders whose chromosome numbers are known are 177 species, and the haploid numbers range between the lowest 4 and the highest 48. Careful comparison of such numbers suggests the presence of some relationship between the chromosome numbers

and general phylogeny. The order Araneae is composed of three suborders Liphistiomorphae, Mygalomorphae and Arachnomorphae. The results obtained show that the chromosome numbers are characteristic of each suborders in considerable degree. The first suborder Liphistiomorphae shows remarkably high number of 48, and the species of the second suborder Mygalomorphae bear  $n=23$ . The members of the third suborder Arachnomorphae have the haploid numbers 4 to 24, but most of the present suborder (i. e. about 90 per cent) are of  $n=4-15$  and the remaining numbers (18-24) occur only in 10 per cent. It seems that in Liphistiomorphae and Mygalomorphae the chromosome numbers are rather constant, although the species studied are not so large. And the number is the highest in Liphistiomorphae and followed by Mygalomorphae. In Arachnomorphae the number is rather low in great majority. Only one part of the group (10%) have exceptionally high numbers similar to Mygalomorphae.

As regards the phylogenetical relationship between the suborders significant results have been obtained by arachnologists. Many authors agree with the opinion that of three suborders the Liphistiomorphae is the oldest in history and the spiders of that suborder exhibit many primitive characters. Concerning these points BRISTOWE ('38) states as follows: "So far as we can judge these spiders (Liphistiidae) are much more closely related to some Carboniferous fossil spiders than they are to any living spiders,"....., and also GERTSCH ('49) describes in his book that the liphistiids are the most primitive of all living spiders, still maintaining the appearance and probably be fundamental structure of their ancient Palaeozoic forebears. It is very interesting that one of such primitive spiders shows an extraordinary high chromosome number and great deviation of chromosome number is found between the liphistiid spider and those of the remaining suborders. This fact suggests that the ancestral primitive spiders might have such remarkable high chromosome numbers and they have been retained in some living descendants such as *Heptathela kimurai*. Therefore such chromosomal condition should be considered to be very old. With regard to the phylogeny of Mygalomorphae there are a few different opinions, but many workers say that the suborder is old next to the Liphistiidae. As mentioned above the species of this group show the second high number.

The Arachnomorphae is considered to have developed in late Carboniferous period. In spite of the latest differentiation the suborder is extremely flourishing at present, which comprises great majority of living spiders. In this suborder the chromosome numbers are reported in 174 species. Of which 156 species, namely about 89% possess relatively low numbers 4 to 15, and the remaining 19 species, namely about 11%, more or less high numbers 18 to 24. That is to say, in the Arach-



nomorphae most species show rather low numbers with some exceptions.

When we consider the relationship between the chromosomes and phylogeny of spiders, it is convenient to classify the chromosome numbers into the following three types: (1) primitive type, (2) intermediate type and (3) modern type.

The first primitive type is known only in one species *Heptathela kimurai*, its chromosome number is extremely high and widely isolated from others. The second intermediate type includes those whose chromosome numbers are 18 to 24, as are found in Mygalomorphae, Sparassidae, Agelenidae, Urocteidae and a few of Argiopidae and Linyphiidae. The last modern type is characteristic of most of modern spiders (Arachnomorphae), the chromosome numbers of this type are less than 15. In phylogenetical viewpoint these three types are arranged from the old to the new in the order of primitive, intermediate and modern type. Thus the chromosome numbers of spiders might have developed from the primitive type, through the intermediate type, to the modern type. In other words, in spiders the chromosomes might have developed from higher condition to lower state. It seems to be concluded that so far as chromosome numbers are concerned, the spiders of Sparassidae, Agelenidae and Urocteidae are old and stand at similar level to the Mygalomorphae. In Argiopidae and Linyphiidae most species bear modern type, only two exceptions *Araneus ventricosus* and *Linyphia montana* show intermediate type. Such conditions suggest that the evolution of chromosome numbers from intermediate type to modern type is actually repeated at present in these families.

Here it is of much interest to consider the chromosome conditions of some closely related orders. By MAKINO's review ('50) the sister orders in which chromosomes have been studied are Xiphosura (OKADA, '38); Scorpionida (CARNOY, '85; SOKOLOW, '13; WILSON, '16, '31; SATO, '36, '40; PIZA, '39 a,b, '41, '43, '44, '47, '48; BRIEZER and GRANER, '43; NATH and GILL, '50; Pseudoscorpionida (SOKOLOW, '26); Pedipalpi (MILLOT and TUZET, '34); Opilionida (SOKOLOW, '29 a, b; TOMOHIRO, '40; SUZUKI, '41) and Acarina (REUTER, '09; NORDENSKIÖLD, '09, '20; SCHRADER, '23; WARREN, '31; SOKOLOW, '34; OPPERMAN, '35; PÄTAU, '36; TUZET and MILLOT, '37; COOPER, '37, '39).

The survey of the published data reveals that the chromosome numbers show rather limited range in most orders, but the Scorpionida is exceptional. In this order the chromosome numbers show great variation, and the number is more or less characteristic of different families. By WERNER ('34) the Scorpionida comprises five families, Buthidae, Scorpionidae, Chactidae, Vejovidae and Bothriuridae. The chromosomes have been studied in about 17 species of these five families. The Buthi-

dae shows  $n=12-13$ ; by PIZA ('39, '41, '43, '44, '46, '47, '48) some of the family with only  $n=3-7$  are shown. In Scorpionidae only a single species is researched, which bears  $n=30-31$ . One species of Chactidae has  $n=28$  to 40. The chromosome numbers of two species of Vejovidae are at least 50 in haploid. On the other hand one species of Bothriuridae shows  $2n=36$ . Thus in Scorpionida the chromosome numbers show such constant range within families. Here also the members of the most modern family Buthidae possess the lowest number, and except Bothriuridae the older families possess the larger number. The relationship between the chromosome number and phylogeny is thus similar to that of spiders. It is very interesting that parallel trend is found in the evolution of chromosome numbers between the both sister orders.

In the following article we want to state the mechanism of such chromosome evolution. However, it is very difficult to give definite conclusion. As is well known in the Diagram I, there exist great deviations in chromosome number between *Heptathela kimurai* and other species. Why have such wide deviations arisen? Here we are compelled to presume the presence of direct relation between the primitive and intermediate types, in other words, we must assume drastic change between them. It may be concluded that the chromosomes of *Heptathela*-condition has been decreased suddenly by some accident, which produced the *Atypus*-like condition. The comparison of chromosomes seems to support this opinion. For example, the chromosomes are very similar in shape and size between the *Heptathela* and *Atypus*. But it is not evident at present why such drastic reduction of chromosome numbers occurs.

Here an alternative explanation may be possible. As fully described before, the mitotic chromosome elements of Sparassidae, Agelenidae and Urocteidae which are of intermediate type are large in size, about twice as large as those of *Heptathela*. Every chromosome of the former is apparently considered to correspond to two or more elements of the latter. It is well known that two acrocentric elements give rise to a metacentric by whole-arm transposition. For example, in Acrididae of 12-chromosome group many species possess 12 acrocentric elements in haploid set, on the other hand, *Philocleon anomalus* (HELVIG, '41) shows 6 metacentrics; between the both extremities exist all gradations. In these cases, however, the rearrangements are  $A_1 + A_2 \rightarrow M$  changes and not  $A_1 + A_2 \rightarrow A_3$  changes. Theoretically it is not always impossible that two acrocentrics give rise one large acrocentric. If we consider two acrocentrics, each consisting of a long limb distal to the centromere and a minute second limb proximal to it, then a break may occur just distal to the centromere in one chromosome and somewhere near distal end in the other. If a mutual translocation takes place there will be a large acrocentric chro-

mosome of twice the original length and a minute body which contains a centromere and a very small region on either side. The former may come to be a permanent member of the chromosome set; the latter will probably be almost completely inert and may be lost in subsequent generations. When such translocations take place in all of the chromosome set of *Heptathela* (as occurred in *Philocleon anomalus*), the condition of intermediate type will arise.

No remarkable deviations in chromosome numbers can be found between the intermediate and modern types, but notable difference exists in the frequencies of chromosome numbers, in particular, we have sharp contrast between the number of 15 and those of intermediate type (see Diagram I). The number of 18 and 19 may be regarded as connecting link between the both types, but in this case also, some drastic reduction of chromosome numbers may be present. The occurrence of such aberrant species as *Araneus ventricosus* and *Linyphia montana* suggests such drastic changes.

As regards the evolution of chromosome numbers within families we have more satisfactory interpretations.

In Pisauridae six species of *Dolomedes* have been studied cytologically, of which four species, i. e. *D. angustivirgatus*, *pallitarsis*, *saganus* and *sulfureus* studied by me possess 13 autosomes and two X's in haploid set. One species *D. fontanus* reported by PAINTER ('14) exhibits equal chromosome number, but contains one pair of microchromosomes (12 A + 1 m + 2 X's) and the remaining *D. fimbriatus* published by HACKMAN ('48) only 11 autosomes and 2 X's. The microchromosomes are found in many species of animals, and some authors insist that they play some significant roles in the evolution of chromosome numbers. Particularly OGUMA ('30) who studied the chromosomes of dragonflies is of opinion that the microchromosomes are degenerating chromosomes, which are in the fate of gradual diminution. A similar interpretation may be applied in the present case. When one pair of autosomes in four Japanese *Dolomedes* species become microchromosomes, the chromosomes of *D. fontanus*-condition will be produced. If such microchromosomes entirely diminish 12 pairs of autosomes in *D. fimbriatus* will be obtained.

A similar condition is found also in the Lycosidae. In the genus *Lycosa* 11 species possess 13 pairs of autosomes, of which one species, *Lycosa tarsalis* reported by HACKMAN ('48) bears one pair of microchromosomes. On the other hand, *L. coelestis* reported in this paper shows the autosomes of 12 pairs instead of 13, furthermore, *L. communis* studied by PAINTER ('14), only 10 pairs of autosomes. Here also the microchromosomes seem to have important meanings in the evolution of chromosome numbers. In this case the evolution might have taken place in the following direction: many *Lycosa* species  $\rightarrow$  *L. tarsalis*  $\rightarrow$  *L. coelestis*

→ *L. communis*. It is of much interest that in both families chromosome numbers show the tendency to decrease as evolution advances.

In addition to the microchromosomes the centric fusion must be highly evaluated. The phenomenon is regarded as to be one of the most important means of chromosomal evolution. Though the favourable examples are relatively few in spiders, it is doubtless that in some spiders the chromosomes have evolved by centric fusion. Concerning this point full description was given in my previous paper (SUZUKI, '51a) and in the foregoing pages of this paper.

### VI. General aspect of sex-chromosomes

Except some earlier reports almost all papers demonstrate the presence of sex-chromosomes in spiders. The spiders are heterogametic in males without exception. The particularities of the sex-chromosomes in spiders are general occurrence of multiple sex-chromosomes. Such elements are not so common to occur in most animals, but in spiders they are very widely found and are possessed by great majority of the present order (Table V).

Table V. Frequency of three types of sex-chromosome mechanisms in 26 families of spiders.

Fam.	XO	XXO	XXXO	Total	Fam.	XO	XXO	XXXO	Total
Liphistiidae		1		1	Oxyopidae	5	1		6
Aviculariidae		1		1	Lycosidae		24		24
Atypidae		1		1	Pisauridae		8		8
Uloboridae		2		2	Agelenidae		6	3	9
Dietyidae		2		2	Argyronetidae		1		1
Amaurobiidae		1		1	Urocteidae		1		1
Dysderidae	1			1	Theridiidae		8		8
Pholcidae		2		2	Linyphiidae		8		8
Drassidae		9		9	Micryphantidae		1		1
Clubionidae		11		11	Tetragnathidae		5		5
Anypaenidae		2		2	Argiopidae		25		25
Sparassidae	1	1	5	7	Mimetidae		1		1
Thomisidae	11	10		21	Total	19	152	8	179
Salticidae	1	20		21	Per cent	10.61	84.91	4.48	

The sex-determining mechanism of an XXO-system was first discovered by WALLACE ('09) and was ascertained in 13 species of spiders by PAINTER ('14), afterwards many authors have reported the validity of such double X-elements in numerous species. By many investigations including the present one the XXO-system is characteristic of 25 families studied with an exception of Dysderidae. Probably further study will demonstrate its presence in Dysderidae. Thus this type is known in 152 species of all the 179 spiders studied (84.91%), and in the 20 families all the species studied possess the present mechanism alone. Contrary to this type, the XXXO-system occurs in limited species, at present it is found in five species of Sparassidae and three of Agelenidae, i. e. totally in eight species (4.48%). It was rather late that a single X-element was found. It is now reported in 19 species (10.61%) of Dysderidae, Sparassidae, Thomisidae, Salticidae and Oxyopidae. This type of sex-determining mechanism is found coexisting with the remaining types within such families; in Thomisidae and Oxyopidae, particularly in the latter it occurs in most members studied.

These three kinds of X-elements are well demonstrated in mitotic and meiotic divisions. In most of gonial divisions, however, accurate identification of X-elements is not easy. WALLACE ('09) reported in the study of *Tegenaria naevia* that the 2 X's are distinguishable during gonial anaphase and telophase, which are lagging others and of larger size. In my experience such figures were never observed. In many cases the X's are regarded as to be the largest elements in the chromosome complements, but the size difference of chromosomes is not so large that it is usually difficult to determine the constant order of size of respective chromosomes.

In the case of XXO-system each of the two X's is of nearly equal size, no size difference can be found, but some exceptions exist in Argiopidae (PÄTAU, '48; HACKMAN, '48; SUZUKI, '51a), Thomisidae (HACKMAN, '48; SUZUKI, '52a) and Lycosidae (HACKMAN, '48; SUZUKI, in this paper). Particularly in the last two families the size difference is often notable. Such feature in Thomisidae was fully reported in my previous paper (SUZUKI, '52a). In Lycosidae all 24 species studied possess 2 X's, which are almost equal in length in 20 cases, but not in the remaining four species, *Trochosa rulicola*, *Lycosa fluviatilis*, *T-insignita* and *cinereofusca*. While in the first three species the difference of both X's is not so large, in *L. cinereofusca* one X differs greatly from the other. The variation of such X-elements very much resembles that found in Thomisidae.

In the case of XO-system also the single X seems to be the largest element in the complements. Contrary to the 2 X's the single X is distinguishable in most of the gonial metaphase. The X-element in

*Misumena*, *Xysticus* and *Coriarachne* of Thomisidae and in *Oxyopes* and *Nishina* of Oxyopidae (SUZUKI, '52a) is the largest one, which exhibits sometimes particular form and considerable degree of negative heteropycnosis in some mitotic spindles. The single X of *Heteropoda sexpunctata* published by BOLE-GOWDA ('52) is of special interest, because it is a metacentric element instead of acrocentric one, as he said the single metacentric X is considered to have derived by the centric fusion of two acrocentric X's in the allied forms.

As stated above the three X's are characteristic for Sparassidae and Agelenidae. The occurrence of this type was first published by SOKOLSKA ('25) in one species of *Tegenaria* and lately it was fairly demonstrated by REVELL ('47) in two species of *Tegenaria domestica* and *derhami*. By REVELL the three X's are distinguishable by their greater length in gonial complements, but generally they are more clearly identified in the meiotic divisions. They are different in length. Judging from his picture (REVELL's Pl. I Fig. 6), one of the 3 X's is remarkably larger than the rest two. Furthermore, he was able to prove the presence of 6 X's in the female by direct observation. The 3 X's of *Tegenaria derhami* were reexamined by HACKMAN ('48). In the present paper one more species of Agelenidae, *Cryphoea silvicola* was proved to have 3 X's. In Sparassidae the probable occurrence of 3 X's was first suggested by HACKMAN ('48), and was fully studied by SUZUKI and OKADA ('50), SUZUKI ('52a) and BOLE-GOWDA ('52). It is worthwhile noting that the morphology of 3 X's is similar through all the species studied. One of the 3 X's is always larger, the remaining two are of similar size, if not quite equal. Although they show some irregularities in arrangement, they always behave as if they were a single X, which go undividedly to one pole in the first division and divide equationally in the second division.

## VII. Evolution of multiple sex-chromosomes

As mentioned just above, in spiders three kinds of sex-determining mechanisms of XO, XXO and XXXO-type are found. What relationship does exist between the three types? Why have such different mechanisms been derived? The problem is of much importance in the interpretation of the evolution of multiple sex-chromosomes. It is, however, speculative in general and it is rather difficult to draw definite conclusions. I will give some criticism for the hypotheses so far published together with my opinion.

Summarizing the opinions of many workers such as WHITE ('40, '48), Revell ('47), PÄTAU ('48), HACKMAN ('48), SUZUKI ('51a, '52a) and BOLE-GOWDA ('50, '52) it may be said that among three types an XXXO-type has most newly derived, probably from an XXO-type. If so, which is more

primitive of XXO and XO-type. As fully described above the 2 X's condition occurs very widely throughout almost all families from old to new, on the other hand, the single X is found at present in Thomisidae, Oxyopidae and other few families, and in such cases the system is coexisting with XXO-mechanism. The distribution frequency of both mechanisms suggests that the XXO-condition is older than the XO-condition. The probable existence of XXO-system in the most primitive family Liphistiidae would support such interpretation. Consequently it may be concluded that the XXO-condition is extremely old, probably it was differentiated in the ancestral forms of the present spiders from original XO-condition in archeic period. Many authors agree with this view. Then how has double X-condition been produced from the original single X?

WHITE ('40, '41) basing the publications of PAINTER ('14) and HARD ('39) regarded the two X's of spiders as to be homologous, for both X's are completely equal in size, and he insisted that the XXO-system was derived by the duplication of a single X in ancestral form. The present day studies including this paper do not support his theory, because concerning the homology of 2 X's no such result can be obtained. Recently PATAU ('48) proposed the alternative theory. He applied the centric fragmentation theory by DARLINGTON ('40) in explaining the origin of XXO-system. He states that the two X-elements with about equal length can not be derived simply by centric fragmentation, firstly the misdivision of centromere takes place in the single X in the ancestors of all present spiders, and is combined with a break near the end of the long arm to produce a long inversion with subsequent breakage of the resulting dicentric chromosome. Further breakage happens near the median of that chromosome and with the healing of a free chromatid end, two X's of nearly similar length are produced. On the other hand, BOLE-GOWDA ('50) insists that the PATAU's hypothesis is incapable of accounting the origin of a single X-element of present day spiders from two X's system, and put forward the different hypothesis. According to him the two X-elements of the present day spiders must have originated in the remote past from the single X condition of the ancestors of spiders by a mutual translocation of the X with a supernumerary centric fragment, the break in the X occurring somewhere in the middle. The resultant two X-elements are of about equal length. The hypothesis of BOLE-GOWDA seems to be ingenious, but no statement was given on the origin of supernumerary centric fragment. My opinion is that as PATAU described, a single X in ancestral spiders might have undergone the misdivision of centromere, which was followed by a large inversion and became a dicentric X, in the middle of which a breakage took place, and thus resulted two X-elements of about equal size. On the other

hand, an XXXO-system may be of newer origin than XXO-system. Surveying the XXXO-system so far studied it is evident that one out of three X's is always larger in size than the rest two, and the latter are usually of similar length. Sometimes the larger X is almost equal to the total of two smaller X's. It is very probable that one larger X of one species with 3 X's corresponds to one X of another species with 2 X's, and the two smaller X's in the former have arisen from the remaining X in the latter by repeating the above mentioned process.

The origin of XO-system in modern spiders from XXO-system may be more clearly explained. A single X of *Heteropoda sexpunctata* reported by BOLE-GOWDA ('52) is metacentric. Most of the allied forms of the family bear three acrocentric X's and the remaining one spider *Olios lamarcki* with two acrocentric X's. Therefore it is highly probable that the metacentric X of *H. sexpunctata* has been derived from the centric fusion of two acrocentric X's in the allied forms. On the other hand, a single X-element of Thomisidae and Oxyopidae is of acrocentric type, consequently its origin ought to be different from the metacentric X. HACKMAN ('48) who first reported the occurrence of a single X in spiders stated that the single X of *Oxyopes ramosus* seems to be metacentric and that probably it has arisen by centric fusion of two free X-elements, but the single X of *Xysticus* and *Misumena* might have originated from the elimination of one of the two X's. The first statement is not right, because his observation of metacentric X-element is somewhat doubtful, in fact by my study a single X of *Oxyopes* is never metacentric but acrocentric, a similar condition was reexamined by BOLE-GOWDA ('50) in Indian material. Regarding the origin of XO-system BOLE-GOWDA ('50) says that the single X-element was evolved by mutual translocation between the two X-elements. A proximal and a distal break in the two X's respectively gave rise to a large acrocentric X and a small centric fragment which was lost in the process. Contrary to his hypothesis the present author agrees with the second possibility of HACKMAN. A number of my findings support the gradual elimination of one of the two X's. In Thomisidae some species bear single X and others 2 X's. And the 2 X's may be either equal or variable in size, moreover, the difference between the 2 X's varies in species. Thus in Thomisidae various gradations of X's are observed between the single X and the two X's of about equal size. It may be concluded that such condition suggests gradual elimination of one X in the course of phylogeny. (Concerning this point see my second paper of this series). Further findings of such condition in Lycosidae would support this view.



## SUMMARY

1. The present paper deals with the chromosomes of 57 species of spiders belonging to 17 families (3 suborders), in addition, general review of chromosomes in spiders and discussion of the evolution of chromosome numbers and sex-chromosomes are stated basing on my study and so far published data.

2. The materials surveyed include three Finnish spiders *Sitticus littoralis* (Salticidae), *Cryphoea silvicola* (Agelenidae) and *Crustulina guttata* (Theridiidae), except which all 54 species are Japanese spiders.

3. The chromosome numbers and sex-determining mechanisms of newly studied species are shown in the Table II.

4. Liphistiidae, Atypidae, Uloboridae, Dysderidae, Urocteidae and Mimetidae are quite new material to cytology, and the chromosomes of Liphistiidae, Atypidae and Dysderidae are particularly worthwhile noting. Especially *Heptathela kimurai*, one of the Liphistiidae bears extraordinarily high chromosome number. It is very interesting that the most primitive species exhibits the highest number of chromosomes.

5. The haploid chromosome numbers range from 4 to 48, but except *Heptathela kimurai* with  $n=48$ , all the remainings show  $n=4$  to 24, thus great deviations of chromosome number exist between the *Heptathela kimurai* and all the remaining species.

6. So far as the phylogenetical relations are concerned, the chromosome numbers are divided into three groups: (1) primitive type, (2) intermediate type and (3) modern type. The primitive type is characteristic of the most primitive family Liphistiidae. The intermediate type is represented by Mygalomorphae families and some of Arachnomorphae, and the modern type is typical to most families of Arachnomorphae. The chromosome number is the highest in primitive type, the second in intermediate type and the lowest in modern type. Thus in spiders the chromosomes show strong trend to decrease in number according to the evolution of phylogeny.

7. In cytological viewpoint Sparassidae, Agelenidae, Urocteidae and Amaurobiidae are exceptional families within Arachnomorphae, because the chromosome numbers of which are of intermediate type. They are considered to be in Mygalomorphae condition. *Linyphia montana* of Linyphiidae and *Araneus ventricus* of Argiopidae are also regarded as to be of such rather old intermediate type.

8. Most species of Arachnomorphae show the haploid number 4 to 15, of which 15, 13 and 12 occur in overwhelming members.

9. The metacentric elements were newly found in *Dictyna foliicola*, *Ariadna lateralis* and *Pholcus crypticolens*, in which all the autosomes are metacentrics. All the remaining species possess acrocentric elements

alone.

10. The meiotic chromosomes of *Ariadna lateralis* are extremely large, one of which is considered to be homologous to two or more chromosomes of allied forms. In these chromosomes the "pellicle"-like structure is clearly observable.

11. The mitotic chromosomes of *Plexippus setipes* and several of the same genus are furnished with seta of varying length.

12. The size of chromosomes and cell plates is generally constant in families, but in some cases it shows considerable variation. *Heptathela kimurai* and *Atypus karschi* possess extremely large cell plates, while their chromosomes are very small, on the other hand, in Arachnomorphae the species with larger chromosomes show in general greater sized cell plates. It seems that some correlation exists between the whole volume of chromosomes and the size of cell plate.

13. All species studied possess sex-chromosomes; regarding sex the males are unexceptionally heterogametic.

14. The sex-chromosome mechanism of an XXO-type is found in 55 species of 16 different families. *Ariadna lateralis* bears single X and Finnish *Cryphoea silvicola* with XXXO-type. Through all the materials the sex-chromosomes are always prereducational.

15. The Japanese *Myrmarachne japonica* shows usual XXO-type, while the Finnish *Myrmarachne formicaria*, XO-type. In Japanese species the presence of 4 X's is clearly recognized in both mitotic and meiotic divisions of the female. It is interesting that the Japanese *Myrmarachne* differs from the Finnish one not only in the X-elements but also in the autosome number, which is 13 pairs in the former and 11 pairs in the latter.

16. The chromosome numbers and 4 X's of females were observed in *Miagrammopes orientalis*, *Myrmarachne japonica*, *Hasarius albarius*, *Pisaura lama*, *Dolomedes angustivirgatus*, *Dolomedes sulfureus* and *Araneus saganus*.

17. In most species studied the 2 X-elements are nearly equal in size, but in *Lycosa T-insignita* and in particular, in *Lycosa coelestis* a great size difference is present.

18. The three X-elements found in *Cryphoea silvicola* very much resemble those of *Tegenaria* and *Heteropoda*.

19. The XXO-type is considered to be very old, and was probably originated in remote past from XO-condition by centric fragmentation accompanying inversion and the following breakage. The XXXO-system is considered to have derived from the XXO-system by repeating the same process as that mentioned just above. On the other hand the XO-system of present day spiders has probably been produced from XXO-condition by gradual elimination of one of the 2 X's.

20. In the evolution of chromosome numbers in Pisauridae and Lycosidae, microchromosomes seem to play some important role.

21. Regarding the polyploidy no definite conclusions are obtainable, but in *Hasarius adansonii* and *Icius magister* tetraploid spermatocytes are found, moreover, in many species of Linyphiidae giant epithelial cells exist in the testes, which are considered to be polyploid cells.

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## EXPLANATION OF PLATES

The figures in Plates were drawn, with the exception noted, at table level with the aid of an ABBE camera lucida, using an objective 120 and an ocular 20, tube length, 180 mm, giving a magnification of ca. 4000 diameters. All the figures were reduced to approximately 2/3 for publication.

### PLATE I.

- Figs. 1-5. *Heptathela kimurai*, spermatogenesis.
- Figs. 1-3. Spermatogonia; Fig. 1 with 96 chromosomes, Fig. 2 95 chr., Fig. 3 94 ones.
- Fig. 4. Primary spermatocyte, metaphase, lateral view.
- Fig. 5. The same, polar view, with 48 chromosomes.
- Figs. 6-12. *Atypus karschi*, spermatogenesis.
- Fig. 6. Spermatogonium, metaphase plate with 44 chromosomes.
- Figs. 7-9. Primary spermatocytes, metaphases; Fig. 7 with 21 autosome bivalents and 2 X's. Figs. 8 and 9 with 21 bivalents, X's are not seen.
- Figs. 10-11. The same, profiles, 2 X's are clearly visible.
- Fig. 12. The same, anaphase, profile.

### PLATE II.

- Figs. 13-26. *Miagrammopes orientalis*. Figs. 13-15 and 18-26 spermatogenesis. Figs. 16-17 oögenesis.
- Figs. 13-15. Spermatogonial metaphases with 22 chromosomes.
- Figs. 16-17. Oögonial metaphases with 24 chromosomes.